

A New Marattialean Fern from the Middle Triassic of Eastern Australia

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The marattialean genus *Marantoidea* Jaeger is revised, and *Danaeopsis* Heer is shown to be a junior synonym of *Marantoidea*. Of the species formerly assigned to *Danaeopsis*, those that can be confirmed as marattialean are transferred to *Marantoidea*; many of the others are probably pteridosperms. The new species *Marantoidea acara* is described from the Middle Triassic Toogoolawah Group and Nymboida Coal Measures of eastern Australia. It is distinguished by the small size of its sporangia. The Triassic distribution of marattialeans in Gondwana indicates that these ferns had a similar temperature preference in the past to that today, and have probably had a megathermal-mesothermal distribution throughout their history.

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INTRODUCTION

The marattialean ferns can be traced back to the Carboniferous, and they have a more or less continuous fossil record from then to the present (Taylor and Taylor 1993). There are 6 extant genera, two of which, *Angiopteris* and *Marattia*, grow in northeast Australia (Camus 1998). In the Mesozoic of the Northern Hemisphere (Laurasia), marattialean ferns were often abundant and formed a significant element of these floras, e.g. Late Triassic of northern China (Chen et al. 1979), Early Jurassic of Japan (Kimura et al. 1992), and Middle Jurassic of Yorkshire (Harris 1961; Hill 1987). The Middle-Late Triassic *Danaeopsis-Symopteris* flora of northern China is partly named after the marattialean fern *Danaeopsis* (Kimura and Ohana 1990).

By contrast, marattialeans were a minor component of Mesozoic Gondwanan floras. They were rare in the Jurassic and Cretaceous, e.g. there are only 2 records, one of them doubtful, from Australian strata of this age (Dettmann and Clifford 1991). In the Triassic of Gondwana marattialeans were more common, but apart from a few localities where they were abundant, they were only ever a small element of these floras. A number of Triassic marattialean genera have been recorded in Gondwana: one from South Africa (Anderson and Anderson 1985), four from South America (Herbst 1977a, 1977b, 1988), and seven from Australia: *Asterotheca* (Herbst 1977a, Holmes this volume), *Marattiopsis* (Playford et al. 1982), *Rhinipteris* (Holmes this volume), *Danaeopsis* (Walkom 1917, 1928), *Ogmos* (Webb 1983), *Eboracia* (Playford et al. 1982), and *Herbstopteris* (part *Rieniisia* of Herbst

1977b; Holmes this volume), although the affinities of the last four are tentative (Dettman and Clifford 1991, and discussion below).

Danaeopsis is reassessed in this paper, which describes a new species of marattialean fern from the Middle Triassic of eastern Australia.

GEOLOGICAL SETTING

In southeast Queensland and northeast New South Wales there are two Middle Triassic basins, the Esk Trough and Nymboida Basin respectively. The Esk Trough contains up to 2350 m of nonmarine conglomerate, sandstone, shale and minor coal, with interbedded andesitic lavas and tuffs (Cranfield et al. 1976). These strata are divided into the Esk Formation, Neara Volcanics and Bryden Formation, there being some degree of lateral equivalence between all three. Palynofloras from drillholes in the southern portion of the basin indicate that the Esk and Bryden Formations are Anisian-Ladinian in age (de Jersey 1975; Helby et al. 1987), confirmed by radiometric dates from lavas within the sequence (236-242±5 Ma, Webb 1982; probably Anisian using the time-scale of Young and Laurie 1996). The Esk Trough strata thin abruptly on the eastern side of the basin against the West Ipswich Fault (O'Brien et al. 1994).

The Nymboida Basin lies to the east of the southern extension of the West Ipswich Fault, and is, therefore, probably separate from the Esk Trough; cover sediments of the Late Triassic-Jurassic Clarence-Moreton Basin obscure the relationship between the two Middle Triassic basins. The Nymboida Basin contains the Nymboida Coal Measures, approximately 1070 m of nonmarine conglomerate, sandstone and shale with interbedded basic volcanics (McElroy 1963, Holmes 2000); the uppermost, thickest unit is the Basin Creek Formation. Attempts to extract identifiable palynofloras from these sediments have been fruitless (de Jersey 1958); the palynomorphs are partly carbonised due to the high temperatures that have affected the coal measures (VR 0.95-0.97; Russell 1994). The macroflora has been correlated with that in the Esk Trough strata, and therefore regarded as Middle Triassic (Flint and Gould 1975). This is verified by radiometric dating of an interbedded basalt flow as probably Anisian (230.7±0.4 Ma; Retallack et al. 1993, using the time-scale of Young and Laurie 1996).

TAXONOMY

Genus *Marantoidea* Jaeger 1827
1827 *Marantoidea* Jaeger, p. 28
1864 *Danaeopsis* Heer, p. 54

Type species

Marantoidea arenacea Jaeger 1827, from the Triassic of Germany; by original designation.

Diagnosis

(Expanded from Schimper 1869) Fronds large, pinnate; pinnae long and lanceolate; secondary veins diverge from midrib at very acute angle, then immediately curve away and run towards the margin at 60°-80° to midrib; each secondary vein usually bifurcates close to the midrib, may fork again and then anastomose near pinna margin. On abaxial side of fertile specimens, biseriate sori, arranged parallel to the lateral venation, extend from midrib to margin; sporangia small, free, circular or elliptical in outline, with longitudinal furrow marking line of dehiscence.

Discussion

There has been some confusion over the correct name and circumscription of this genus. Jaeger (1827) erected the genus and species *Marantoidea arenacea*, which

Table 1. Comparison of *Marantoidae* species for which fertile material is available (n.d. = no data).

species and references	occurrence (age, locality)	pinnæ			basiscopic margin decurrent	secondary venation		sporangia		spacing between adjacent sori
		max. width (mm)	max. length (cm)	spacing (cm)		anastomoses	density (veins/10 mm)	size (mm)	apical depression	
<i>M. arenacea</i> (Jaeger 1827) comb. nov. Schenk (1864), Schimper (1869), Leuthardt (1904)	Middle-Late Triassic Europe	45 to 65	18 to 30	8 to 9	yes	occasional	10 to 13	0.5 x 0.5	no	yes
<i>M. lucensis</i> (Stur 1885 ex Krasser 1909) comb. nov. Krasser (1909)	Late Triassic Austria	15 to 22	18 to 20	3	yes	occasional	10	0.7 x 0.7	n.d.	n.d.
<i>M. fecunda</i> (Halle 1921) comb. nov. Halle (1921), Neuberg (1959)	Late Triassic Sweden, Russia	25 to 30	> 10	4	no	occasional - frequent	10 to 12	0.65-1.0 x 0.8-1.2	yes	no
<i>M. fecunda</i> (Halle 1921) comb. nov. Herbst (1977b, 1988)	Late Triassic Argentina	23 to 58	> 16	5 to 6	n.d.	occasional	9 to 16	0.9-1.0 x 0.9-1.0	?yes	no
<i>M. hallei</i> (P'an 1936) comb. nov. P'an (1936), Tsao (1965) Sze (1956), Li, Tsao & Wu (1976) Sze & Lee (1951)	Late Triassic China	17 to 65	> 18	2 to 8	yes and no	frequent	10 to 15	0.3-0.5 x 0.4-0.8	yes	no
<i>M. emarginata</i> (Brik 1952) comb. nov. Brik (1952)	Triassic Kazakhstan	12 to 45	11	n.d.	yes	rare	12 to 20	0.4 x 0.4	n.d.	?no
<i>M. petchorica</i> (Khamova & Pavlov 1971) comb. nov. Khamova & Pavlov (1971)	Early Triassic Russia	20 to 35	n.d.	n.d.	n.d.	occasional	10 to 15	0.3-0.7 x 0.3-0.7	no	no
<i>M. acara</i> Webb sp. nov.	Middle Triassic Australia	22 to 32	> 18	3 to 5	yes	rare - occasional	12 to 14 (sterile) 18 to 20 (fertile)	0.15 x 0.2	no	no

Presl (1838) renamed *Taeniopteris marantacea*. In 1845 Presl erected *Danaeopsis* for a species of modern fern; Heer (1864) used the same name for a new genus with the type species *D. marantacea* (Presl) Heer, but this is clearly a later homonym. Krasser (1909) and Halle (1921) argued that *M. arenacea* should be discarded in favour of *Danaeopsis marantacea* because the former name had fallen into disuse, the type species of *Marantoidea* is sterile whereas that of *Danaeopsis* is fertile, and the name *Marantoidea* was derived from the supposed resemblance of the fossil to the extant monocot *Maranta*. Nevertheless, under Article 51 of the International Code of Botanical Nomenclature (Greuter et al. 1993), "an alteration of the diagnostic characters or of the circumscription of a taxon does not warrant a change in its name", the name *Marantoidea* is valid and has priority over later homonyms.

A number of species of *Danaeopsis* and *Marantoidea* are known, but only seven of these, for which fertile pinnae have been described, can be validly assigned to *Marantoidea* (Table 1). The differences between many of these species are small, and further study could show some of them to be synonymous. It should be noted that of the five species of *Danaeopsis* described by Brik (1952), only one, *D. angustipinnata* Brik 1952, includes fertile material, but the holotype of this species is sterile; the fertile specimens differ in pinna width and vein density from the holotype, and are referable to *D. emarginata* Brik 1952.

Of the other species previously referred to *Danaeopsis*, *D. sp. cf. cacheutensis* Kurtz 1921, described by Frenguelli (1938), probably belongs to a new marattialean genus, but better preserved material is necessary before this can be erected. *D. cacheutensis* Kurtz 1921, *D. rajmahalensis* Feismantel 1877, *D. hughesii* Feismantel 1882 and *D. gracilis* Lele 1962 are pteridosperms (Lele 1962, Herbst 1977b, Retallack 1977). Probably three separate species have been described as *D. hughesii*; the Indian species (Feismantel 1882; Lele 1962) is different from the Australian specimens (Walkom 1917, 1928), and both differ from the material from China and Kazakhstan (P'an 1936, Brik 1952). The two species described by Prinada and Turutanova-Ketova (1962), *D. rarinervis* Turutanova-Ketova 1962 and *D. taeniopteroides* Turutanova-Ketova 1962, are both sterile and could be cycadophytes.

Amongst the extant marattialean ferns, *Marantoidea* is closest to *Archangiopteris*, but differs in that the latter has well-spaced sori that do not extend to either the midrib or pinna margin (Bower 1926).

Marantoidea acara Webb sp. nov.

Figs 1A-D, 2

Diagnosis

Anastomoses in secondary veins rare; sporangia very small (0.2 mm x 0.15 mm), with no spacing between adjacent sori.

Description

Fronds are relatively large, with a short petiole and a rachis 6-7 mm wide, from which opposite to subopposite pinnae diverge at angles of 45°-60° every 3-5 cm (Figs 1A,B). Individual pinnae are 22-32 mm wide and at least 18 cm long and taper gradually to an acute apex. At the base of each pinna the acroscopic pinna margin is markedly contracted, whereas the basiscopic margin is decurrent on the rachis (Figs 1B,2). Midveins of pinnae are up to 3.5 mm wide; secondary veins diverge at very acute angles but curve away almost immediately and run fairly straight and parallel to the margin at an angle of 60°-80° to the midrib. Most secondary veins fork once close to the midrib, rarely to occasionally a second time, in which case they anastomose with an adjacent vein near the margin. Density of venation is 12-14 veins per 10 mm in sterile fronds. In fertile material the veins are denser, 18-20 per 10 mm.

On fertile pinnae the abaxial surface of the leaf is covered with small (0.2 x 0.15 mm) ellipsoidal sporangia (Fig. 1C), with long axes perpendicular to the lateral venation. Each sporangium has a prominent longitudinal slit, and no visible apical depression (Fig. 1D). The sporangia are relatively well-spaced and are arranged in rows roughly parallel

Figure 1. *Marantoidea acara* sp. nov., UQF71052, from UQL4224, holotype, fertile frond. A,B: adaxial surface, note decurrent pinnae bases. C,D: abaxial surface, note arrangement and morphology of sporangia.

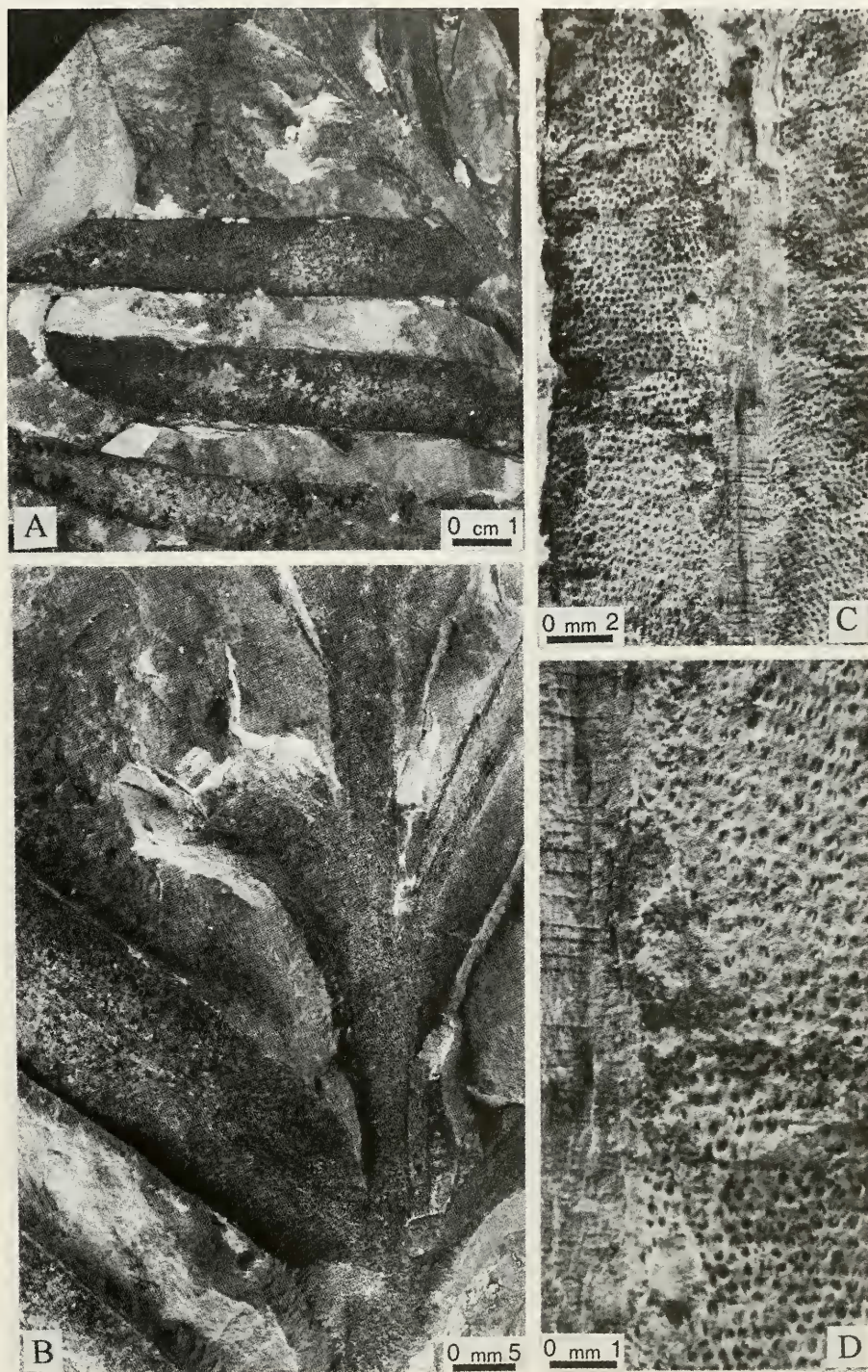


Figure 2. *Marantoidea acara* sp. nov., AMF 113388, from UQL3745, sterile frond; note scale bar in top left corner (divisions in cm).



to and overlying the venation, but are not obviously differentiated into sori; spacing between rows is fairly uniform.

Holotype

UQF 71052, Palaeontological Collection, Queensland Museum (formerly housed in Department of Earth Sciences, University of Queensland).

Type Locality

UQL 4224, hillside, 594893 Somerset Dam 1:50,000 sheet, Bryden Formation, Toogoolawah Group, Esk Trough, Queensland; Anisian – Ladinian.

Other Material

UQF 71053 from the type locality and AMF 113387-113390, AMF 113449 from UQL 3745, Coal Mine Quarry, Basin Creek Formation, Nymboida Coal Measures; Anisian – Ladinian.

Etymology

acares - Greek for small or tiny. A reference to the small sporangia.

Discussion

Sterile foliage of *M. acara* is readily identifiable, despite the lack of sporangia, by its similarity in size, shape and venation to fertile fronds. The adaxial surfaces of fertile specimens show these features clearly. Sterile fronds of *M. acara* resemble some other *Marantioidea* species (Table 1), but fertile specimens are readily distinguished by the considerably smaller sporangia.

PALAEOCLIMATIC SIGNIFICANCE

Living marattialeanes are exclusively tropical and subtropical, i.e. megathermal-mesothermal using the broad-scale temperature regime terminology of Nix (1982). In eastern Australia the most widely distributed living species extends to only ~ 30°S (Camus 1998). In the Middle Triassic marattialeanes had a much broader distribution; the Esk Trough and Nymboida Basin lay at about 60°S (Veivers 2000), and the other Gondwana locations where marattialeanes have been recorded (El Tranquilo Basin, South America; Karoo Basin, South Africa) were at similar palaeolatitudes. Overall, the Triassic climate was considerably warmer than at present (Frakes 1979), and in the Middle Triassic of the northern hemisphere, mesothermal floras characterised by pteridophytes and cycadophytes extended to 70°N (Ziegler et al. 1993). The Middle Triassic climate at 60°S in eastern Australia was probably humid and mesothermal, based on the diverse flora, containing many large-leaved species (Balme et al. 1995). The extensive development of fluvial sedimentation, with some coal measures (Yeates et al. 1986), indicates a more humid climate and higher water tables than in the Early Triassic, when red-beds were deposited across eastern Australia. Thus the occurrence of marattialeanes in these relatively high latitude eastern Australian Triassic floras is consistent with the humid megathermal-mesothermal distribution of extant representatives of this family.

In the Late Triassic and Jurassic of the northern hemisphere, the highest diversity, humid mesothermal floras containing numerous fern genera, including marattialeanes, lay at 40-50°N (Ziegler et al. 1993). The relative scarcity of Gondwanan marattialeanes of this age may reflect the fact that there are relatively few megafloreal localities known from equivalent southern palaeolatitudes.

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